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REGENERATION IN HYDRACTINIA AND PODOCORYNE.

ANNAH PUTNAM HAZEN.

IN a paper entitled "Experiments in Regeneration and in grafting of Hydrozoa,"[1] Peebles has given the results of some interesting experiments with Hydractinia and Podocoryne. These two hydroids are found at Woods Hole on the shells inhabited by hermit crabs. Each colony consists of three different kinds of individuals, namely, the nutritive, the reproductive, and the protective (a low cone-shape growth extending over the hydrorhiza is considered by some authors to constitute a fourth class of individuals). The experiments described by Peebles were confined to the first three classes. The well-marked characteristics of the different kinds of individuals make it possible to distinguish between them even when the polyps are immature or incompletely regenerated. The knoblike tentacles of the reproductive polyps appear during regeneration earlier than the reproductive organs, and the long, slender tentacles of the nutritive polyps can be easily distinguished from those of the protective individuals, which contain nematocysts. Peebles found that polyps freed from the hydrorhiza would live for days in small dishes containing sea water and quickly regenerate lost parts. Pieces of the stalk of these three classes of polyps, from which the heads had been cut, regenerated new heads of the same kind as those that had been removed. Small pieces cut at different levels from the stock of nutritive and protective polyps regenerated at one end a head like the one removed. Not infrequently a head appeared at both ends of a short piece. Without exception, the regenerated heads had the same characteristics as those that had been removed, and no constant variation in time or capacity for regeneration at the different levels was observed.

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[1] *Archiv für Entwickelungsmechanik der Organism*, Bd. x, Hefte 2, 3.

Nutritive polyps cut from the hydrorhiza were grafted by Peebles in pairs, either by their oral ends (after removing both heads) or at the aboral ends (with both heads attached), or the aboral end of one individual was grafted to the oral end of another, from which the head had been removed. In all cases the line of union between the two components was soon effaced, the digestive cavities became continuous, and a complete union seemed to be effected. In all the experiments in grafting nutritive polyps, nutritive heads were regenerated at one or at both ends, and often also in the region of the graft. The union of different kinds of individuals was also successfully accomplished as follows: The aboral end of a nutritive polyp was grafted to the aboral end of a protective polyp,—the direction of the two components being thus reversed. After a few hours the nutritive head was removed, leaving a portion of its stalk attached to the aboral end of the protective polyp. The head which regenerated at the free cut surface showed markedly the characteristics of the nutritive individual and did not seem to be in the least affected by union with the protective polyp. Similar grafts were made with nutritive and reproductive polyps, followed by a removal of the reproductive head. Here, again, the regeneration of a reproductive head at the end of the stalk showed no modification due to the union with a nutritive polyp.

The results of these experiments by Peebles suggested the following questions: first, Would the fixation by means of stolons of one of the components of the graft alter the result? second, Would the kind of regeneration that took place be affected by the relative orientation (with respect to the polarity) of the pieces? With these questions in mind, I carried out the following series of experiments at the Marine Biological Laboratory during a few weeks in July and August, 1901.

Both Hydractinia and Podocoryne were used, and the method of grafting was similar to that employed by Peebles. It was found to be of importance to use fresh material, since that kept for several days in the aquarium regenerated more slowly and less constantly than material just brought in. A few experiments like those described by Peebles were repeated and similar results obtained, although most of the grafts were made by joining the aboral end of a reproductive polyp to the oral end of a nutritive stalk, the head of the latter having been previously removed. In this way the direction of the two components was the same, instead of reversed, as in Peebles's experiments. The pieces were allowed to remain undisturbed for a short time after grafting, or until the tissues had become united, so that the reproductive head could be cut off without danger of separating the grafted pieces. Better results seemed to be obtained if the head were removed within a few hours after union, so that the process of regeneration started in the first night after the graft had been made, although satisfactory results were sometimes obtained when the cut was made on the second day. Fig. 1 represents a typical experiment of this kind. An immature reproductive polyp (*r.*) was selected and grafted at its aboral end to the oral end of a nutritive stalk (*n.*) from which the head had been removed. The tissues joined, and a few hours later the reproductive head was removed, leaving the two components of nearly equal size. Within twenty-four hours a complete reproductive head had regenerated (*rh.*), which showed no modification due to the influence of the stalk of the nutritive polyp.

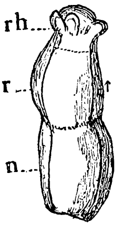

Fig. 1. — × 45. The aboral end of an immature reproductive polyp (*r.*) was grafted to the oral end of a nutritive stalk (*n.*) August 3. A few hours after the union, the reproductive head was cut off, as indicated by the dotted line. The next day a reproductive head (*rh.*) had regenerated on the end of the reproductive stalk. (Drawn August 5.) The arrows point toward the oral end of each individual.

When the union of the two components was incomplete and a part of the cut surface of the nutritive stalk was exposed at the side, tentacles or a whole nutritive head developed at this place, as shown in Figs. 2, 3, and 4, *nt.* This occurred frequently, as the nutritive polyps are often much larger than the reproductive polyps, and the latter, unable to cover the whole cut surface, unite with the nutritive only at one side. This did not prevent the body cavities of the two components from becoming continuous. The portion of the reproductive stalk (*r.*) used in the experiment shown in Fig. 2 was taken from the oral region of a young individual, while the nutritive component (*n.*) came from the aboral region and shows a piece of a spine (*s.*) attached to its base. Although, in this case, the nutritive component was relatively much larger than the reproductive stalk, a head regenerated on the latter which showed no apparent influence of the larger component but possessed only the characteristics of the reproductive head.

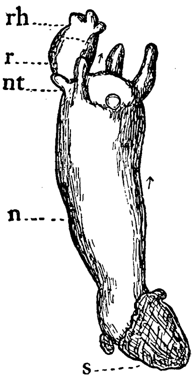

FIG. 2. — × 45. The aboral end of a young reproductive polyp (*r.*) was grafted to one side of the oral end of a nutritive stalk (*n.*) August 3. A few hours later the reproductive head was cut off as indicated by the dotted line, leaving a small portion taken from the oral half of a reproductive individual attached. A reproductive head (*rh.*) regenerated at the end of the reproductive stalk and nutritive tentacles (*nt.*) around the end of the nutritive stalk. A piece of spine (*s.*) was attached to the base. (Drawn August 5.)

Another experiment is shown in Fig. 3 in which the nutritive stalk (*n.*) was many times larger than the small component taken from a reproductive polyp (*r.*). The latter was cut from the aboral region of an adult individual from which most of the generative buds had been removed.[1] Here, again, the union was complete, and again the regenerated head showed no effect produced by the larger component, but the new growth corresponded to what would probably have appeared on a reproductive stalk alone from which the head had been removed.

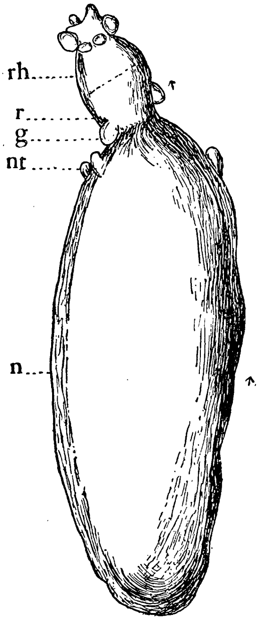

FIG. 3. — × 45. The aboral end of a reproductive polyp (*r.*) was grafted, July 25, to the oral end of a nutritive stalk (*n.*). Three hours later the reproductive head was removed at a place indicated by the dotted line. The reproductive component which remained was from the aboral region of an adult. Two generative buds (*g.*) were left attached; others had been removed. A reproductive head (*rh.*) and nutritive tentacles (*nt.*) developed. (Drawn July 27.)

Many similar experiments were made, from which these have been selected as typical. Considering that these different individuals are organically connected, it seemed at the outset possible that, under certain conditions where a complete union was effected, the subsequent regeneration might be modified. This seemed especially likely to occur if the nutritive polyp, which is the more vigorous and the less specialized of the two, formed the larger component. Repeated attempts were made to leave as small a portion of the reproductive stalk as possible attached to the nutritive component, but, with one exception, none were obtained in which the regenerated head showed the influence of the nutritive polyp. The result is the same when the direction of the two components is reversed, as in Peebles's experiments, and when it is the same, as in most of my experiments (see Figs. 1, 2, and 3). All regions of the stalk from which the components are taken seem equally unable to influence the subsequent regeneration or to be influenced by the union. It was also found that the regeneration following a graft of this sort is no more easily influenced when the reproductive component is taken from an immature polyp than when it is taken from an adult.

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[1] Two generative buds were left, as shown in Fig. 3, *g.*

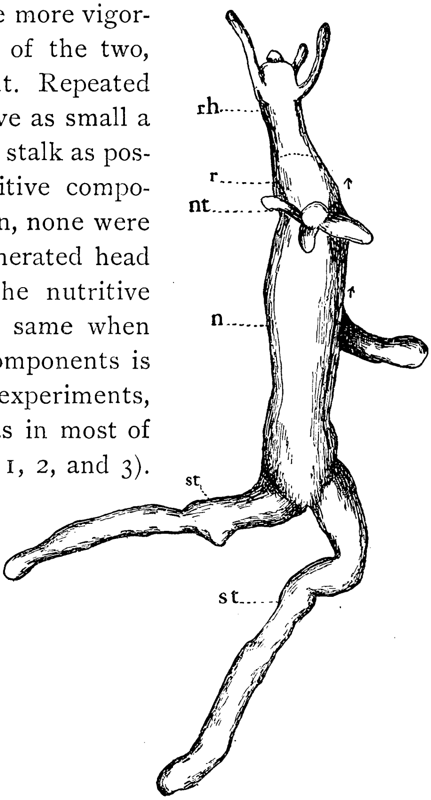

Fig. 4. — × 45. The aboral end of a reproductive polyp (*r.*) was grafted to the oral end of a nutritive stalk (*n.*) July 20. The reproductive head was cut off July 21, as indicated by the dotted line. The next day a nutritive head (*rh.*) had regenerated on the end of the reproductive stalk and nutritive tentacles (*nt.*) at the point of union between the two components. Stolons (*st.*) had also developed on the aboral end of the nutritive stalk attaching it to the disk. (Drawn July 23.)

An interesting and solitary exception to these results is illustrated in Fig. 4. A nutritive polyp (*n.*) and a reproductive polyp (*r.*) were grafted as in the preceding cases, and on the following day the reproductive head was removed, leaving only a small part of the reproductive stalk attached. A day later a nutritive head (*rh.*) had regenerated on the end of the reproductive component and, at the same time, stolons (*st.*) had pushed out from the nutritive polyp, fastening it to the bottom of the dish. As this was the only instance in which a reproductive polyp produced a nutritive head, it was probable that a new condition had appeared and affected the regeneration. What this condition may have been was not satisfactorily determined, but a possible explanation was suggested by comparison with the results of another series of experiments carried on at the same time. These will be described below.

Peebles showed that pieces of the stalk of nutritive polyps cut free from the colony and allowed to remain undisturbed at the bottom of a shallow dish of water sometimes sent out long branching stolons, the original stalk becoming absorbed and indistinguishable from the newer growth. "After several days new individuals began to appear, growing up at right angles to the stolons, just as the different individuals of a colony grow from the hydrorhiza. The formation of new polyps continued for several weeks when the experiments were brought to an end. As many as ten to fifteen new polyps were produced by one piece of the stalk. These polyps were invariably nutritive individuals, characterized by their long slender tentacles." I repeated this experiment and also used pieces of nutritive polyps as well as pieces of the stalk. The growth of a large number of colonies followed. New nutritive polyps were always the first to appear on the stolons,

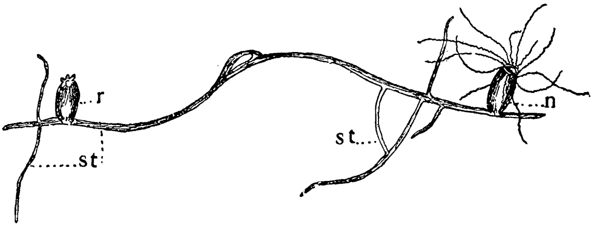

FIG. 5. — Represents a small portion of a colony which had developed from a nutritive polyp, showing a new nutritive polyp (*n.*), a reproductive polyp (*r.*), and stolons (*st.*). The original polyp had been absorbed. The colony was started July 24. The drawing was made August 3. The disintegration of the colony began August 8.

but after the colony was well formed a few small reproductive polyps also grew out from the stolons at occasional intervals (Fig. 5). Although the colony lived for several days or a week after the production of the reproductive polyps, no signs of developing generative buds appeared. Indeed, the life of the colony seemed spent, the stolons became more slender and broke apart, and the polyps died, one after another. During the period of growth the stolons often anastomose and two adjacent colonies become united. Such colonies are most easily started if whole polyps are cut off close to the hydrorhiza. A small piece of a polyp will lie on its side on the bottom of the dish, often producing new hydranths and changing its form, until it disintegrates, but rarely forms stolons.

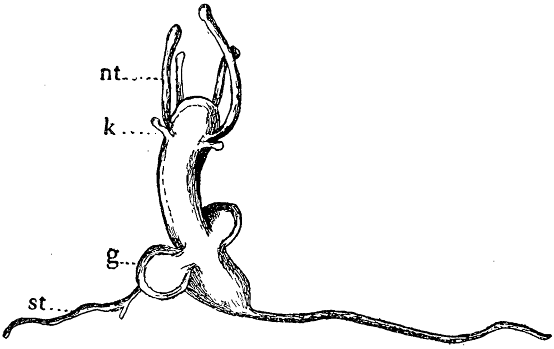

FIG. 6. — Represents a reproductive polyp which was cut from the hydrorhiza July 20. Several generative buds were removed; two were left (*g.*). The reproductive tentacles were replaced by four nutritive tentacles (*nt.*). Two small knoblike tentacles (*k.*) are seen below the nutritive tentacles. At the same time the nutritive tentacles were developing, stolons (*st.*) grew from the aboral end, fastening the individual to the disk. (Drawn July 23.)

In the same way reproductive polyps were removed and kept in dishes, with the hope that they would also form colonies. They sent out stolons much more slowly than the nutritive polyps did, and although a large number of individuals formed stolons, many of them died before new polyps had developed. It is probable that others, which seemed more vigorous, might have developed new polyps had more time been allowed them. In one dish in which half a dozen reproductive polyps had formed stolons a curious change was observed. The stolons had grown rapidly, and the hydranths which had borne the small knob characteristic of the reproductive polyp showed, in three days, a remarkable development of tentacles like those on a nutritive hydranth, as shown by *nt.*, Fig. 6. Two small knobs (*k.*) are present below the ring of tentacles, and these may — or may not — represent those of the original reproductive hydranth. A few large generative buds had been removed from the polyp, but two remained as seen in Fig. 6, *g*. The polyps seemed vigorous, but possibly the presence of the generative buds caused an early disintegration. At all events, they all died before any new polyps were formed by the stolons. What the condition was which brought about this change was not determined, but it seemed possible that the formation of stolons might be connected with the development of nutritive tentacles. The growth of stolons in this case (Fig. 6) was more rapid than in that of other reproductive individuals in which the nutritive tentacles did not develop. In other instances the reproductive heads may have lost the power of developing the long tentacles when the stolons were late in appearing. A clearing up of this point might throw light on the experiment described above (Fig. 4), in which a piece of a reproductive stalk grafted to a nutritive polyp regenerated a nutritive head. The reproductive head had not been removed until the day following the graft, and the stolons developed at the same time that the head was regenerated. The regeneration of the nutritive head might have been influenced by the developing stolons.

It gives me pleasure to acknowledge my indebtedness to Prof. T. H. Morgan for many suggestions during the course of this work.

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